



Dietary variability of extinct tayassuids and modern white-lipped peccaries (*Tayassu pecari*) as inferred from dental microwear and stable isotope analysis



Jennifer L. Bradham^{a,*}, Larisa R.G. DeSantis^{a,*}, Maria Luisa S.P. Jorge^{a,b}, Alexine Keuroghlian^c

^a Department of Earth and Environmental Sciences, Vanderbilt University, Nashville, TN 37235, United States

^b Department of Biological Sciences, Vanderbilt University, Nashville, TN 37235, United States

^c Peccary Project/IUCN/SSC Peccary Specialist Group, MS, Brazil

ARTICLE INFO

Keywords:

Climate change
Dietary plasticity
Peccary
Generalist
Ungulates

ABSTRACT

Prior geochemical work documents dietary shifts coincident with climate change in extinct peccaries, with taxa typically shifting between browsing and mixed-feeding. This study employs dental microwear texture analysis (DMTA) and stable carbon isotopes to interpret the diet of extinct peccaries in Florida, specifically *Platygonus*, *Mylohyus*, and *Protherohyus* from the late Miocene throughout the Pleistocene, to evaluate how dietary behavior has fluctuated over time. When *Mylohyus* and *Protherohyus* coexisted in the Hemphillian, *Mylohyus* consumed C₃ food sources with harder textures, consistent with the consumption of woody browse, while *Protherohyus* consumed a greater proportion of C₄ vegetation (likely grass). During the Blancan, both *Platygonus* and *Mylohyus* can be considered primarily C₃ browsers, based on both DMTA and stable isotope data. However, during the Irvingtonian, both *Mylohyus* and *Platygonus* consumed a larger proportion of C₄ vegetation than during previous North American Land Mammal Ages (NALMAs). *Platygonus* consumed predominantly C₃ vegetation during the Rancholabrean, while *Mylohyus* consumed a mixture of C₃ and C₄ vegetation in more open environments. Independent of NALMA, *Platygonus* consumed predominantly tough vegetation, (e.g., tough leaves and/or grass) while *Mylohyus* consumed harder food items, consistent with morphological differences in their teeth. In contrast, extant *Tayassu* peccaries are obligate C₃ feeders and show no evidence of C₄ consumption. Further, *Tayassu* are indistinguishable in all dental microwear textural properties from both of their extinct relatives, suggesting that while extant peccaries eat primarily foods from forested environments, those foods are highly variable in textural properties. Collectively, these data suggest that extinct peccaries, *Mylohyus* and *Platygonus*, altered their diet over time and possibly in response to changing climates.

1. Introduction

Over time, members of the Tayassuidae (commonly referred to as ‘peccaries’) have occupied a diverse array of habitats including moist tropical forests, tropical savannas, and closed canopy woodlands in North, South, and Central America (e.g. Altrichter and Boaglio, 2004; Keuroghlian et al., 2009; MacFadden and Cerling, 1996; Wetzel et al., 1975). However, after the end of the Pleistocene, tayassuid ranges largely became restricted to Mexico, Central America, and South America, with isolated populations of collared peccaries found in the southwestern United States (Altrichter et al., 2001; IUCN, 2017; Torres et al., 2016; Wetzel et al., 1975).

As some extant members of this family, e.g. *Tayassu*, can cause unique top-down effects on their ecosystems through herding

behaviors, seed predation and dispersal, and the requirement of large home ranges (Beck, 2006; Fragoso, 1998; Keuroghlian et al., 2009; Keuroghlian and Eaton, 2008; Reyna-Hurtado et al., 2015), understanding tayassuid ecology both today and in the past can provide information on how dietary preferences have changed both over time and in response to past climate fluctuations. Further, knowledge of how extinct peccary diets compare to those of extant taxa can elucidate the degree to which peccary diet was generalized over time and can provide an understanding of how dietary preferences of modern tayassuids may fluctuate in response to current and future climate change events.

Modern *Tayassu* are highly frugivorous (e.g. Altrichter et al., 2001; Desbiez et al., 2009; Keuroghlian and Eaton, 2008). However, they have also been documented as consuming additional foliage in times of food scarcity (Keuroghlian et al., 2009; SOWLS, 1984). Further, the

* Corresponding authors.

E-mail addresses: Jennifer.l.bradham@vanderbilt.edu (J.L. Bradham), larisa.desantis@vanderbilt.edu (L.R.G. DeSantis), malu.jorge@vanderbilt.edu (M.L.S.P. Jorge).

amount of fruit in modern *Tayassu* diets varies with geographic location and tracks fruit availability (Beck, 2006). However, whether dietary generalism has always been present among tayassuids and the degree to which extinct and extant peccaries share similar dietary patterns remains unclear. Assessing dietary ecology and variability over deep time requires multiple methods capable of capturing different aspects of diet (e.g. textural properties and isotopic composition). Coupling multiproxy paleoecological information from the fossil record with ecological studies can provide information on dietary ecology over time.

Here, we integrate multiple paleoecological methods including morphological data, dental microwear texture analysis (DMTA), and geochemical analyses to clarify the ecology of fossil peccaries as well as modern *Tayassu* peccaries at a variety of spatial and temporal scales, including since the Plio-Pleistocene and between North and South America. Specifically, we test the following hypotheses:

- i. Tayassuids from the late Miocene throughout the Pleistocene were dietary generalists, consuming browse and mixed vegetation in Florida.
- ii. Extinct sympatric genera were able to coexist because they consumed disparate diets and hence represent different dietary niches, as inferred from stable isotopes and DMTA.
- iii. When compared to their extinct counterparts, extant tayassuids exhibit similar degrees of dietary variability, as inferred from stable isotopes and DMTA.

2. Background

2.1. Evolutionary history of Tayassuidae

Tayassuids, suiform artiodactyls, are distantly related to pigs, hogs, and boars (Wright, 1998). Three species of extant tayassuids currently exist: the white-lipped peccary (*Tayassu pecari* Link 1795), the collared peccary (*Pecari tajacu* Linnaeus 1758), and the chacoan peccary (*Catagonus wagneri* Rusconi 1930). The majority of evidence suggests that tayassuids first appeared during the late Eocene of North America (Wright, 1998). While some suggest tayassuids are represented in South America during the late Miocene (e.g. Campbell et al., 2010 and sources therein), unequivocal skeletal evidence indicates that tayassuids are definitively recorded in South America by the late Pliocene (Cione et al., 2015; Gasparini, 2013).

Phylogeny between extinct and extant tayassuids remains unresolved; however, it is a topic of active research (Parisi Dutra et al., 2017; Prothero, 2015). To date, the most complete assessments of peccary relationships comes from Wright (1989) and Parisi Dutra et al. (2017). Using morphological data, Wright (1989) separated the tayassuids into two monophyletic clades, one composed of *Platygonus*, *Mylohyus*, and *Tayassu*, and the second comprised of *Catagonus* and *Pecari*. Through genetic and morphological analyses, Parisi Dutra et al. (2017) suggested the genus *Catagonus* is polyphyletic, such that *Catagonus brachydontus* is the sister group to *Platygonus*, and *Mylohyus*, while *Catagonus wagneri* is most closely related to *Tayassu*. Due to the paraphyletic nature of the genus *Catagonus*, we hereafter refer to *Catagonus brachydontus* with the newly designated nomenclature of *Protherohyus brachydontus* (Parisi Dutra et al., 2017). Other research based on dentition posits *Protherohyus* and *Catagonus* may be most closely related to *Platygonus* (Wetzel et al., 1975). A genetic assessment consisting solely of extant species concluded *Tayassu pecari* and *Pecari tajacu* form a monophyletic clade, with *Catagonus wagneri* equally related to both (Gongora and Moran, 2005). If the phylogeny of Wright (1989) is correct, peccaries likely underwent multiple separate migrations from North America to South America since the Pliocene, as Miocene representatives of *Platygonus* and Pleistocene *Pecari* are preserved in North American deposits (Hulbert et al., 2009; Wright, 1998). Perhaps the best-known and well-described fossil peccaries are those from the late Miocene through the Pleistocene, *Protherohyus*, *Mylohyus*, and

Platygonus, and as such will be the focus of this study. Further, the extant genus, *Tayassu* (commonly referred to as the white-lipped peccary), is included as a modern taxon with a potential generalized diet based on observational data and fecal analyses (e.g. Altrichter et al., 2001; Keuroghlian and Eaton, 2008).

2.2. Paleoecology of extinct peccaries

Although many tayassuid fossil remains have been described, limited studies have undertaken paleoecological assessments of extinct peccaries. Those that have, center on morphological information (e.g. Hulbert, 2001) with some additional studies using geochemical data to infer tayassuid paleoecology (D'Amo, 2001; DeSantis et al., 2009; Feranec, 2005; Feranec and DeSantis, 2014; Feranec and MacFadden, 2000; Koch et al., 1998; MacFadden and Cerling, 1996; Trayler et al., 2015; Yann et al., 2016; Yann and DeSantis, 2014). Additionally, there is only one dental microwear study of tayassuid fossil remains, *Platygonus compressus* from southern Indiana (Schmidt, 2008). Through a two-dimensional dental microwear analysis, the author concluded that the species' diet was similar to those of browsers or mixed-feeders, consuming both hard and soft food materials as well as abrasive and non-abrasive foods (Schmidt, 2008).

Cheek teeth of *Protherohyus* and *Platygonus* are zygodont, having sharply angular crests associated with primary cusps, with those of *Platygonus* being more hypsodont than the former (Wright, 1989). In contrast, *Mylohyus* has bunodont teeth, those with rounded cusps (Wright, 1998). General morphological interpretations of diet based on dentition suggest *Platygonus* may have consumed cactus and coarse-vegetation, while *Mylohyus* preferred fruit, nuts, and softer vegetation or were browse/browse-dominated mixed feeders (Hulbert, 2001; Webb, 1974; Webb et al., 2008; Wright, 1998). This would largely restrict *Mylohyus* to being a forest-dwelling taxon and suggests that *Platygonus* occupied more open environments, such as prairies (Webb, 1974).

Most stable isotope analyses of extinct peccaries in North America center around sites in Florida, where they are abundant and well preserved (D'Amo, 2001; DeSantis et al., 2009; Feranec, 2005; Feranec and DeSantis, 2014; Feranec and MacFadden, 2000; Koch et al., 1998; MacFadden and Cerling, 1996; Yann et al., 2013; Yann and DeSantis, 2014). Stable isotope analyses of *Platygonus* and *Mylohyus* enamel from Pleistocene glacial and interglacial localities of Florida indicate *Platygonus* was a C₃ browser during a glacial period (Ingles 1A, FL), even though C₄ grasses were present (DeSantis et al., 2009). However, *Platygonus* transitioned to mixed feeding during an early Irvingtonian (~1.6 to 1 Ma) interglacial period (Leisy Shell Pit 1A) and consumed both C₃ browse and C₄ grass (DeSantis et al., 2009). DeSantis et al. (2009) did not analyze *Mylohyus* during known glacial periods due to lack of specimens at Ingles 1A but note that the genus consumed a mixture of C₃ and C₄ vegetation during interglacial times. *Mylohyus* consistently consumed C₃ vegetation during the latest Pleistocene in Florida, as evidenced by isotopic analysis of specimens from Vero Beach 2 ($\delta^{13}\text{C}$ values of -10.8‰ and -10.9‰) and Cutler Hammock ($\delta^{13}\text{C}$ values of -11.4‰ , -10.0‰ , and -8.0‰ ; Koch et al., 1998). Additional isotopic studies categorize *Platygonus* as a mixed feeder during the first half of the Pleistocene and then strict browser starting in the middle Irvingtonian (~1.0 to 0.6 Ma; Feranec and MacFadden, 2000). Feranec and MacFadden (2000) and DeSantis et al. (2009) suggested this shift occurred in response to the appearance of a second mixed-feeding peccary, *Mylohyus*, or a shift in flora; yet, morphological interpretations suggest that *Mylohyus* was likely a browser (Webb et al., 2008). Work by Yann and DeSantis (2014) indicate that both *Platygonus* and *Mylohyus* were browsing or mixed feeding at additional Pleistocene sites (Haile 8A and Tri-Britton) in Florida. Based on carbon isotopes of tayassuids from Florida throughout the Pleistocene, the consumption of moderate amounts of CAM plants or C₃ grasses by *Platygonus* and *Mylohyus* was possible (MacFadden and Cerling, 1996), although unlikely

due to the rarity of CAM plants and C_3 grasses in Florida (Koch et al., 1998; Stowe and Teeri, 1978; Teeri and Stowe, 1976). *Platygonus compressus* from Ingleside (Texas) has carbon isotope values consistent with the consumption of C_3 browse in more open environments and/or mixed feeding of both C_3 browse and C_4 grass (values of -9.1‰ and -8.8‰ ; Yann et al., 2016). Further, Trayler et al. (2015) report one stable carbon isotope value of -13.5‰ for *Platygonus vetus* at a mid-Irvingtonian aged site in California, Fairmead Landfill. With the exception of one specimen from the Love Bone Bed of Florida (MacFadden and Cerling, 1996), the dietary ecology of extinct *Protherohyus* specimens in North America have not yet been extensively studied using geochemical techniques.

2.3. Ecology of extant peccaries

Modern *Tayassu* cheek teeth are bunodont and clear correlations between tooth morphology and diet have not been demonstrated in extant tayassuids (Wright, 1998), suggesting additional methods are needed to fully correlate diet between extinct and extant taxa. While *Tayassu* have been recorded in seasonally inundated wetlands, dry tropical forests, and tropical savannas, (e.g. Keuroghlian and Eaton, 2008; Keuroghlian et al., 2009), they are found primarily in moist, tropical forests from southern Mexico to Argentina. They are considered largely frugivorous, and often consume palm fruits and seeds (Altrichter et al., 2001; Keuroghlian and Eaton, 2008; Keuroghlian et al., 2009; Kiltie, 1981a, 1981b; Wright, 1998) with analyses from stomach contents suggesting that palm seeds alone can account for over 60% of *Tayassu* diet (Beck, 2006; Bodmer, 1990; Kiltie, 1981b). Additionally, *Tayassu* consume a greater diversity of fruits during the wet season, when more fruits are available (Keuroghlian et al., 2009). During periods of low fruit availability or food scarcity, vegetative plant parts including stems, leaves, and roots have been documented as constituting up to 39% of stomach contents (Barreto et al., 1996; Desbiez et al., 2009; Kiltie, 1981b). A small portion of stomach contents ($< 1\%$) even consisted of consumed animal materials (Kiltie, 1981a) and additional studies have noted a preference of seeds infected with bruchid beetle larvae (Fragoso, 1994; Jansen, 2003; Kiltie, 1981b; Silvius, 2002).

2.4. Dental microwear texture analysis

Dental microwear texture analysis quantifies microscopic features via scale-sensitive fractal analysis on the chewing surface of teeth that have resulted from food processing (e.g. Scott et al., 2005, 2006; Ungar et al., 2003). DMTA reflects the textural properties of an organism's diet within the last few days to weeks of an animal's life (Grine, 1986) and can distinguish between consumption of foods that are soft and tough compared to those that are hard and brittle (Calandra and Merceron, 2016; DeSantis, 2016; Scott et al., 2005, 2006; Ungar et al., 2003). Tough foods, such as grasses and some leaves, are resistant to crack propagation and are therefore best broken down by blade-like structures and shearing motions (e.g. shearing cusps; Strait, 1997). Hard foods are those that break or crack such as seeds, nuts, and woody browse, such that the harder the food, the more resistant it is to cracking (Strait, 1997). An additional descriptive term, abrasiveness, describes a food's ability to create abrasions on the wear surface of the tooth (Calandra and Merceron, 2016).

Resulting scale-sensitive fractal analyses from DMTA generate the following informative parameters: anisotropy ($epLsar$), complexity ($Asfc$), heterogeneity of complexity ($HAsfc$), and textural fill volume (Tfv ; Scott et al., 2005, 2006). Greater anisotropy values in herbivores result from the consumption of tougher food items like leaves or grass, while greater complexity values indicate consumption of harder and/or more brittle food items like woody browse, seeds, or fruit pits (e.g. DeSantis et al., 2017; DeSantis, 2016; Hedberg and DeSantis, 2017; Jones and DeSantis, 2017; Scott, 2012). Heterogeneity of complexity

($HAsfc$) measures the variation among textural features across a surface, while textural fill volume (Tfv) numerically reflects both the shape and texture of the surface, specifically the concavity and convexity (Scott et al., 2006). A surface with greater concavity or convexity will have a greater Tfv value as compared to a more planar surface (Scott et al., 2006).

Initial analyses of microscopic wear features in mammals used scanning electron microscopes or optical microscopes to quantify the relative number of pits and scratches, with increased pits indicative of the consumption of hard food items and a high proportion of scratches demonstrating a diet rich in abrasive food items, such as grass consumption for herbivores (e.g. Semperebon et al., 2004; Solounias and Semperebon, 2002; Walker et al., 1978). However, at times, these methods can be subject to observer error and inconsistent in data replication (DeSantis et al., 2013; Grine et al., 2002; Muhlbachler and Beatty, 2012). While these initial dental microwear studies were seminal in our understanding of ancient diets via microscopic wear patterns on teeth, the 3D analysis of wear features, as demonstrated with DMTA, is better able to distinguish between disparate dietary niches, reduce observer bias, and improve reproducibility (DeSantis et al., 2013). Further, assessment of microscopic wear features through DMTA has been successfully employed to evaluate the textural properties of diet in a diverse assemblage of mammals (e.g. DeSantis, 2016 and references therein).

2.5. Geochemical data

Whereas dental microwear reflects diet over the last few days to weeks of an organism's life, stable carbon isotopes in tooth enamel reflect diet during the time over which enamel was mineralized, on the order of weeks to months, a time period much earlier in life than that reflected by microwear analysis (Hoppe et al., 2004). Stable carbon isotopes recovered from enamel hydroxyapatite can aid in assessing the proportion of C_3 or C_4 plants consumed, as well as clarifying relative forest density (Cerling et al., 2004; DeSantis and Wallace, 2008; van der Merwe and Medina, 1989, 1991). Carbon values from diet are recorded in mammalian enamel with a fractionation factor of -14.1‰ for moderately sized herbivores (Cerling and Harris, 1999). When comparing with modern taxa, there is an additional 1.5‰ subtracted from each stable carbon isotope value for extinct specimens to account for increased CO_2 emissions since the industrial revolution, the Suess Effect (Cerling et al., 1997; Cerling and Harris, 1999; Passey et al., 2005). Stable carbon isotope values of below -9‰ indicate a diet primarily composed of C_3 plant material, while values greater than -2‰ indicate a diet primarily composed of C_4 plants, in extinct peccaries (Cerling et al., 1997; Kohn, 2010). Values falling between those two end members reflect a mixed-feeding diet in extinct taxa (Cerling et al., 1997; Cerling and Harris, 1999; Kohn, 2010). Likewise, stable isotope values below -10.5‰ or above -3.5‰ indicate a predominantly C_3 or C_4 diet, respectively, in modern taxa.

When coupled, stable isotopes and DMTA have the ability to distinguish between C_3 and C_4 browsing and grazing diets (e.g. Prideaux et al., 2009; DeSantis et al., 2017), as well as document changes in textural properties of food consumed, even when isotopic breadth is similar (e.g. Jones and DeSantis, 2017).

3. Materials and methods

3.1. Sample collection

Specimens of extinct taxa, *Protherohyus*, *Platygonus*, and *Mylohyus*, were sampled for DMTA and geochemical analysis from the vertebrate paleontology collections at the University of Florida (Supplementary Tables 1 and 2). For stable isotope analysis of extinct genera, we analyzed a total of 115 teeth including 8 *Protherohyus*, 58 *Platygonus*, and 49 *Mylohyus*. We sampled 126 specimens for DMTA including 22

Protherohyus, 72 *Platygonus*, and 32 *Mylohyus* (Table S2). In Florida, *Mylohyus* specimens spanned the late Miocene (Hemphillian) to late Pleistocene (Rancholabrean), while *Platygonus* specimens have been recovered from the Pliocene (Blancan) to Pleistocene (Rancholabrean; Hulbert, 2001). In Florida, *Protherohyus* is known only from the Hemphillian.

Extant *Tayassu* specimens were sampled from collections at the Museu de Zoologia da Universidade de São Paulo (MZUSP) as well as skulls donated for use by the Wildlife Conservation Society, Brazil (WCS, Brazil) and Dr. Sandra Calvacanti from the Brazilian Institute for the Conservation of Neotropical Carnivores (CENAP, Brazil). We analyzed 14 *Tayassu* microwear samples from MZUSP and 9 samples from WCS and CENAP (Supplementary Tables 1 and 2). No isotope samples were taken from specimens at MZUSP. Rather, 35 teeth were drilled from the WCS and CENAP collections. Because of this, all *Tayassu* specimens drilled for isotopic analysis are primarily from more open-canopy biomes of central Brazil (Pantanal and Cerrado), whereas *Tayassu* specimens evaluated for microwear analysis also included specimens from closed-canopy biomes (Amazonian and Atlantic forests; Olso et al., 2001).

3.2. DMTA

Microwear analyses followed procedures outlined in Scott et al. (2006). Molars, M/m1 or M/m2, were cleaned and molded with a polyvinylsiloxane dental material. After drying, molds were taken back to Vanderbilt University and each sample was put into a stable basin from which to create a cast. Tooth replicates were then made using epoxy (Epotek 301) and examined at Vanderbilt University on a Plu Neox Profiler with white light at 100× magnification. Specifically we scanned a 276-μm × 204-μm area of enamel on the occlusal surface of the protocone (–id). When the protocone (–id) was not preserved or did not exhibit a testable wear stage, the hypocone (–id) was scanned. Only on a few instances were alternate areas of a molar scanned. The scanned area was then divided into a 2 × 2 grid, representing a total of four scans. The median value between the four scans was used to analyze surficial wear features using Toothfrax and Sfrax software packages, software designed specifically for analyzing three-dimensional microscopic wear patterns on teeth.

3.3. Geochemical analysis

To sample and chemically prepare specimens for stable isotope analysis, we followed similar procedures to DeSantis et al. (2009). We selectively bulk sampled (drilled a line of enamel perpendicular to the growth axis of the tooth) M/m1 or P/p4 with a low-powered drill and collected the resulting enamel powder, approximately 2 mg. Chemical preparation of samples occurred at Vanderbilt University where enamel powder was reacted with 30% hydrogen peroxide for at least 24 h, facilitating the removal of organic material. After removing hydrogen peroxide, samples were rinsed with distilled water to remove any remaining hydrogen peroxide residue. We then placed 0.1 N acetic acid in each vial for 18 h to remove diagenetic carbonates, after which the samples were rinsed with distilled water again, dried, and subsequently mailed to the University of Florida Stable Isotope Facility in the Department of Geological Sciences. There, the processed enamel powders were analyzed within ± 0.1‰ analytical precision using a VG Prism stable isotope mass spectrometer with an in-line ISOCARB automatic sampler. All samples were normalized to the laboratory standard (NBS-19 with a δ¹³C value of 1.95‰ vs. PDB) and are reported in traditional delta notation δ¹³C = [(¹³C/¹²C_{sample})/(¹³C/¹²C_{standard}) – 1] × 1000 using the V-PDB standard (Coplen, 1994). An additional 1.5‰ has been subtracted from carbon isotope values of extinct fossil taxa to account for increased emissions since the industrial revolution and facilitate comparison to modern *Tayassu* specimens (e.g. an isotope value of –12.0‰ for an extinct specimen becomes –13.5‰ to facilitate

comparison to its modern counterpart).

We also compiled published data on *Tayassu* stable carbon isotopes in enamel from peccaries in Florida and incorporated those into our analyses (Table S1; D'Amo, 2001; DeSantis et al., 2009; Feranec, 2005; Feranec and DeSantis, 2014; Feranec and MacFadden, 2000; Koch et al., 1998; MacFadden and Cerling, 1996; Yann and DeSantis, 2014).

3.4. Statistical methods

With the exception of isotopic data from *Protherohyus*, results from DMTA and isotopic analyses were confirmed by a Shapiro-Wilk test to follow a non-normal distribution (Supplementary Table 3). However, given the small sample size of *Protherohyus* and the need to compare the genus with other genera, we used non-parametric statistical tests for all analyses. All statistical analyses were done in R, version 3.31 (R Core team, 2013) using Mann-Whitney *U* test when comparing two taxa and Dunn's procedure (Dunn, 1964) when comparing more than two groups. *p*-Values < 0.05 were considered significant. We also calculated summary statistics including mean, median, standard deviation, maximum value, minimum value, and range. We compared each of the DMTA variables (*Asfc*, *epLsar*, *Tfv*, *HASfc*_{3×3}, and *HASfc*_{9×9}) and stable carbon isotope values between Florida peccaries exclusive of North American Land Mammal Age (NALMA), among co-occurring genera within a single NALMA, for a single genus over multiple NALMAs, and between extinct and modern peccaries.

4. Results

4.1. DMTA

Dental microwear texture analysis summary statistics are outlined in Tables 1–2 and Fig. 1, with all temporal and taxonomic comparisons noted in Table 3 and Supplemental Tables 4 and 5.

Collectively, excluding NALMA subsampling, *Mylohyus* yields the largest mean complexity value (6.666) and has a complexity range of

Table 1
Summary statistics of DMTA attributes per taxonomic group.

Genus	Statistic	n	<i>Asfc</i>	<i>epLsar</i>	<i>Tfv</i>	<i>HASfc</i> _{3×3}	<i>HASfc</i> _{9×9}
<i>Mylohyus</i>	Mean	32	6.666	0.0022	13603	0.512	0.957
	Median		4.716	0.0020	13394	0.482	0.825
	SD		5.279	0.0010	2176	0.248	0.444
	Maximum		24.085	0.0038	17918	1.424	2.263
	Minimum		0.933	0.0007	7699	0.160	0.296
	Range		23.152	0.0032	10219	1.264	1.967
<i>Platygonus</i>	Mean	72	4.816	0.0029	12612	0.445	0.847
	Median		2.468	0.0025	13232	0.376	0.764
	SD		5.151	0.0016	3380	0.265	0.485
	Maximum		22.774	0.0073	19873	1.725	3.293
	Minimum		0.447	0.0003	2147	0.181	0.317
	Range		22.327	0.0070	17726	1.544	2.976
<i>Protherohyus</i>	Mean	22	3.306	0.0026	11796	0.641	0.982
	Median		2.577	0.0024	12150	0.567	0.896
	SD		3.046	0.0011	3432	0.448	0.487
	Maximum		13.792	0.0050	16313	2.261	1.929
	Minimum		0.451	0.0006	0	0.203	0.406
	Range		13.341	0.0044	16313	2.058	1.523
<i>Tayassu</i>	Mean	23	4.916	0.0026	13358	0.446	0.789
	Median		2.887	0.0021	13373	0.436	0.718
	SD		4.347	0.0013	1745	0.221	0.368
	Maximum		16.800	0.0061	15964	0.882	1.504
	Minimum		1.681	0.0008	9081	0.124	0.254
	Range		15.118	0.0053	6884	0.759	1.249

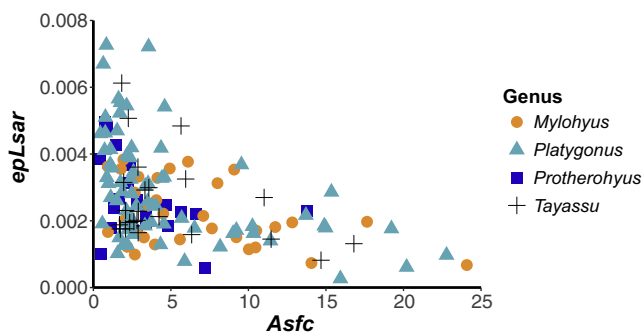
Asfc, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, textural fill volume; *HASfc*_{3×3}, *HASfc*_{9×9}, Heterogeneity of complexity in a 3 × 3 and 9 × 9 grid, respectively; SD, standard deviation (n – 1); Range, total range of all samples examined.

Table 2

Statistical comparisons (p-values) for all DMTA attributes between taxa.

		<i>Mylohyus</i>	<i>Platygonus</i>	<i>Protherohyus</i>
<i>Asfc</i>	<i>Platygonus</i>	0.003		
	<i>Protherohyus</i>	0.002	0.175	
	<i>Tayassu</i>	0.104	0.168	0.063
<i>epLsar</i>	<i>Platygonus</i>	0.018		
	<i>Protherohyus</i>	0.067	0.455	
	<i>Tayassu</i>	0.159	0.239	0.317
<i>Tfv</i>	<i>Platygonus</i>	0.074		
	<i>Protherohyus</i>	0.020	0.143	
	<i>Tayassu</i>	0.367	0.186	0.056
<i>Hasfc_{3x3}</i>	<i>Platygonus</i>	0.027		
	<i>Protherohyus</i>	0.224	0.005	
	<i>Tayassu</i>	0.144	0.309	0.047
<i>Hasfc_{9x9}</i>	<i>Platygonus</i>	0.070		
	<i>Protherohyus</i>	0.483	0.091	
	<i>Tayassu</i>	0.074	0.364	0.086

Asfc, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, textural fill volume; *Hasfc_{3x3}*, *Hasfc_{9x9}*, Heterogeneity of complexity in a 3 × 3 and 9 × 9 grid respectively. Bold denotes significance (p < 0.05).

**Fig. 1.** Scatterplot comparing the DMTA parameters of complexity (*Asfc*) and anisotropy (*epLsar*) for *Protherohyus*, *Mylohyus*, *Platygonus*, and *Tayassu*.

23.152, while *Protherohyus* has the smallest mean complexity value (3.306) and a complexity range of 13.341 (Table 1). *Mylohyus* has significantly higher complexity than both *Platygonus* (p = 0.0034) and *Protherohyus* (p = 0.002; Table 2). In contrast, *Mylohyus* has significantly lower anisotropy than *Platygonus* (p = 0.044), but not *Protherohyus* (Table 2). *Platygonus* has lower heterogeneity of complexity than both *Mylohyus* (p = 0.040) and *Protherohyus* (p = 0.012) at the 3 × 3 scale; yet, there are no significant differences between genera in heterogeneity of complexity at the 9 × 9 scale (Table 2). *Mylohyus* has a higher mean texture fill volume than *Protherohyus* (p = 0.020) but does not differ from *Platygonus* (Table 2).

A comparison between DMTA features for *Tayassu* and each extinct taxa reveals there are no significant differences in any DMTA features between *Tayassu* and any of the extinct genera with the exception of *Hasfc_{3x3}*, where *Tayassu* demonstrates lower mean values than those of *Protherohyus* (p = 0.047; Tables 1–2).

DMTA variables of extinct peccaries were also compared among genera, through time. Mean complexity values for *Mylohyus* appear to generally increase over time from the Hemphillian to the Rancholabrean (Table 3). During the Hemphillian, *Mylohyus* complexity values were lower than during the Blancan (p = 0.013) and Rancholabrean (p = 0.007) (Table S4). Texture fill volume values in the Hemphillian were lower in the Irvingtonian (p = 0.047) and the Blancan (p = 0.016), but not the Rancholabrean (Table S4). *Mylohyus* does not exhibit any other textural differences in dental microwear attributes between the Hemphillian and Rancholabrean (Table S4). There are no significant differences in any dental microwear feature over time for *Platygonus* (Table S5). As *Protherohyus* fossils in Florida are only recorded from the early Pliocene (Hemphillian), temporal

comparisons for this genus were not possible.

Summary statistics of DMTA attributes of co-occurring genera in each NALMA can be found in Table 3. *Mylohyus* and *Protherohyus* co-occur during the Hemphillian and do not significantly differ in any DMTA attribute during this time period (Table S6); *Platygonus* fossils are not present in high enough densities during the Hemphillian in Florida to facilitate inclusion into this analysis. *Mylohyus* and *Platygonus* co-occur during the Irvingtonian, Blancan, and Rancholabrean NALMAs (Table 3). During the Irvingtonian and Blancan, *Mylohyus* and *Platygonus* have indistinguishable DMTA attribute values with the exception of *Mylohyus* having higher mean *Hasfc_{3x3}* values than *Platygonus* during the Irvingtonian (p = 0.028; Table S7). During the Rancholabrean, *Platygonus* had a lower mean complexity value (4.349) than *Mylohyus* (8.348; p = 0.025).

4.2. Stable carbon isotopes

Results from carbon isotope analyses are found in Tables 4–6, and Fig. 2. When all isotopic values are pooled together (regardless of NALMA), *Mylohyus*, *Platygonus*, and *Protherohyus* all demonstrated similar mean $\delta^{13}\text{C}$ values that are indistinguishable from one another (Tables 4–5). *Mylohyus* had a range of 12.0‰, while *Protherohyus* and *Platygonus* had ranges of 6.3‰ and 10.6‰, respectively (Table 4). However, when comparing co-occurring genera in each NALMA, $\delta^{13}\text{C}$ values were not always indistinguishable (Fig. 2, Table 6). During the Hemphillian, *Mylohyus* had a lower mean $\delta^{13}\text{C}$ value (−13.5‰) than *Protherohyus* (−10.6‰; p = 0.032). During the Blancan, both *Platygonus* and *Mylohyus* had similar $\delta^{13}\text{C}$ values (−12.8‰ and −13.9‰, respectively; Table S4). While $\delta^{13}\text{C}$ values for *Platygonus* and *Mylohyus* in the Irvingtonian are indistinguishable (p = 0.518), *Platygonus* had a lower mean $\delta^{13}\text{C}$ value (−13.0‰) than *Mylohyus* (−11.0‰) during the Rancholabrean (p = 0.002; Table 6).

An evaluation of *Mylohyus* through time reveals that during the Hemphillian and Blancan *Mylohyus* had similar mean $\delta^{13}\text{C}$ values (−13.5‰ and −13.9‰, respectively; Table S8). Yet, mean $\delta^{13}\text{C}$ values from *Mylohyus* in the Hemphillian are lower than those of *Mylohyus* in the Irvingtonian (p = 0.003) and Rancholabrean (p = 0.003). Similarly, mean $\delta^{13}\text{C}$ values in the Blancan were also lower than the Irvingtonian (p = 0.006) and the Rancholabrean (p = 0.009). However, *Mylohyus* stable carbon isotope values during the Rancholabrean and the Irvingtonian do not differ from each other, nor do they differ between the Hemphillian and the Blancan (Table S8). *Platygonus* has lower mean $\delta^{13}\text{C}$ values during the Blancan, as compared to the Irvingtonian (p = 0.011), yet not the Rancholabrean (p = 0.355), as Rancholabrean values are lower than those of the Irvingtonian (p = 0.0002).

While all extinct peccaries evaluated have similar mean $\delta^{13}\text{C}$ values exclusive of NALMA, *Tayassu* has a lower mean $\delta^{13}\text{C}$ value than any of the extinct genera (after accounting for the Suess effect, see Materials and Methods; Tables 4–5).

5. Discussion

5.1. Extinct peccaries

Of the tayassuids sampled, only *Protherohyus* and *Mylohyus* were evaluated during the Hemphillian NALMA due to the limited availability of specimens for study. As indicated by lower $\delta^{13}\text{C}$ values, *Mylohyus* consumed food items from a more closed environment than *Protherohyus* (van der Merwe and Medina, 1989, 1991). Further, higher mean *Asfc* values indicate *Mylohyus* also consumed harder food items than *Protherohyus* (Scott et al., 2005, 2006; Ungar et al., 2003). Collectively, these results suggest *Mylohyus* may have been a C₃ frugivore and/or consumed a greater proportion of woody browse (including hard twigs), consistent with morphological interpretations (Hulbert, 2001; Webb et al., 2008). The wide range of $\delta^{13}\text{C}$ values for

Table 3

Summary statistics of all DMTA attributes separated by taxonomic group and North American Land Mammal Age (NALMA).

		Hemphillian		Blancan		Irvingtonian		Rancholabrean		Modern
		<i>Mylohyus</i>	<i>Catagonus</i>	<i>Mylohyus</i>	<i>Platygonus</i>	<i>Mylohyus</i>	<i>Platygonus</i>	<i>Mylohyus</i>	<i>Platygonus</i>	<i>Tayassu</i>
<i>Asfc</i>	Mean	3.045	3.306	7.901	3.445	6.053	5.072	8.348	4.349	4.916
	Median	2.786	2.577	10.454	1.690	4.284	2.497	7.645	2.898	2.887
	SD	1.834	3.046	4.170	3.917	4.572	5.304	6.277	5.210	4.347
	Maximum	7.087	13.792	11.734	10.322	12.827	22.774	24.085	20.200	16.800
	Minimum	0.941	0.451	2.673	0.447	2.815	0.578	0.933	0.724	1.681
	Total range	6.146	13.341	9.060	9.874	10.012	22.196	23.152	19.476	15.118
<i>epLsar</i>	Mean	0.0023	0.0026	0.0018	0.0031	0.0021	0.0028	0.0023	0.0032	0.0026
	Median	0.0023	0.0024	0.0017	0.0026	0.0021	0.0025	0.0020	0.0025	0.0021
	SD	0.0009	0.0011	0.0009	0.0023	0.0004	0.0014	0.0012	0.0020	0.0013
	Maximum	0.0036	0.0050	0.0033	0.0067	0.0026	0.0073	0.0038	0.0072	0.0061
	Minimum	0.0012	0.0006	0.0010	0.0008	0.0016	0.0003	0.0007	0.0006	0.0008
	Total range	0.0023	0.0044	0.0023	0.0059	0.0010	0.0070	0.0032	0.0066	0.0053
<i>Tfv</i>	Mean	12,482	11,796	14,757	11,209	14,545	12,948	13,566	11,802	13,358
	Median	12,572	12,150	14,855	11,292	14,806	13,367	13,297	11,481	13,373
	SD	2186	3432	1218	3663	1666	3287	2371	3639	1745
	Maximum	16,781	16,313	16,447	15,669	16,145	19,873	17,918	19,021	15,964
	Minimum	9421	0	13,026	5109	12,422	2147	7699	5028	9081
	Total range	7360	16,313	3421	10,559	3723	17,726	10,219	13,993	6884
<i>HAsfc_{3×3}</i>	Mean	0.551	0.641	0.501	0.686	0.593	0.428	0.474	0.399	0.446
	Median	0.422	0.567	0.422	0.366	0.580	0.379	0.479	0.344	0.436
	SD	0.403	0.448	0.131	0.619	0.032	0.209	0.215	0.180	0.221
	Maximum	1.424	2.261	0.649	1.725	0.639	1.129	0.987	0.884	0.882
	Minimum	0.160	0.203	0.393	0.234	0.572	0.181	0.229	0.233	0.124
	Total range	1.264	2.058	0.255	1.492	0.067	0.948	0.758	0.651	0.759
<i>HAsfc_{9×9}</i>	Mean	1.108	0.982	0.832	1.379	1.049	0.797	0.895	0.802	0.789
	Median	0.806	0.896	0.800	0.788	1.048	0.773	0.777	0.738	0.718
	SD	0.740	0.487	0.089	1.245	0.213	0.319	0.356	0.388	0.368
	Maximum	2.263	1.929	0.942	3.293	1.283	1.680	1.605	1.872	1.504
	Minimum	0.296	0.406	0.722	0.364	0.815	0.317	0.397	0.400	0.254
	Total range	1.967	1.523	0.220	2.929	0.468	1.363	1.209	1.472	1.249

Asfc, area-scale fractal complexity; *epLsar*, anisotropy; *Tfv*, textural fill volume; *HAsfc_{3×3}*, *HAsfc_{9×9}*, Heterogeneity of complexity in a 3 × 3 and 9 × 9 grid respectively; SD, standard deviation (n – 1). Range, total range of all samples examined.

Table 4

Summary statistics for stable carbon isotope analysis (V-PDB, ‰) between genera. Data summarized here include both newly collected data as well as data from MacFadden and Cerling (1996), Koch et al. (1998), Feranec and MacFadden (2000), D'Amo (2001), Feranec (2005), DeSantis et al. (2009), Feranec and DeSantis (2014), and Yann and DeSantis (2014).

	<i>Protherohyus</i>	<i>Mylohyus</i>	<i>Platygonus</i>	<i>Tayassu</i>
n	8	49	58	35
Mean	–10.6	–11.4	–11.3	–14.4
Median	–11.1	–12.0	–12.0	–14.5
SD	2.5	2.5	2.7	0.7
Maximum	–7.3	–3.8	–4.8	–12.7
Minimum	–13.6	–15.8	–15.4	–15.5
Total range	6.3	12.0	10.6	2.8

n is sample size; SD, standard deviation (n – 1). Values have been corrected for the Suess effect (–1.5 ‰ in extinct taxa as compared to modern taxa).

Table 5

Statistical comparisons (P-values) for stable carbon isotope analysis between all studied taxa. Values from extinct genera accounted for the Suess effect (–1.5‰) prior to comparison.

	<i>Mylohyus</i>	<i>Platygonus</i>	<i>Protherohyus</i>
<i>Platygonus</i>	0.467		
<i>Protherohyus</i>	0.213	0.198	
<i>Tayassu</i>	< 0.0001	< 0.0001	< 0.0001

p-Values < 0.05 are considered significant and noted here in bold.

Protherohyus (–13.6‰ to –7.3‰) suggests that *Protherohyus* consumed both C₃ and C₄ material. As C₃ grasses and C₄ shrubs are rare in Florida (Koch et al., 1998; Stowe and Teeri, 1978; Teeri and Stowe, 1976), these data suggest that *Protherohyus* consumed both browse and

grass.

While *Protherohyus* fossils are not recorded in Florida after the Hemphillian, *Mylohyus* persists in Floridian deposits throughout the Pleistocene (Hulbert, 2001). During the Hemphillian, *Mylohyus* consumed softer food items than during the Rancholabrean (p = 0.007) and Blancan (p = 0.013) as evidenced by lower mean *Asfc* values in the Hemphillian. *Mylohyus* also exhibited lower *Tfv* values (p = 0.016) during the Hemphillian as compared to the Blancan, indicating that microwear features had lower volumes during the Hemphillian. Stable carbon values from *Mylohyus* in the Hemphillian and Blancan are significantly lower than those of the Irvingtonian and Rancholabrean, indicating *Mylohyus* was foraging in more open environments in the Pleistocene as compared to the late Miocene or Pliocene. Collectively, these results suggest *Mylohyus* had a diet comprised of primarily C₃ browse and/or fruit and consumed hard objects throughout the late Miocene to early Pliocene. As complexity values for *Mylohyus* are higher in the Rancholabrean and the genus is potentially consuming food items in more open environments, increased complexity values may also be indicative of increased grit consumption (Janis et al., 2002; Kaiser and Schulz, 2006). However, recent research has shown that the dietary signal overwhelms any signal created by dust or phytoliths (Merceron et al., 2016), so these changes in complexity are most likely indicative of dietary differences.

After the disappearance of *Protherohyus* at the end of the Pliocene, *Platygonus* becomes more prominent and coexists with *Mylohyus* in Florida throughout the Pleistocene (Hulbert, 2001). When comparing the two genera independent of NALMA, higher *epLsar* values suggest *Platygonus* was consuming tougher food items than *Mylohyus* (p = 0.044), potentially tough leaves and/or grass. The higher complexity values seen in *Mylohyus* suggest the genus consumed harder food items than *Platygonus* (p = 0.009, Table 2). These results are consistent with morphological differences between these taxa. *Mylohyus*

Table 6

Summary statistics of stable carbon isotope values (V-PDB, ‰) of all extinct taxa during different NALMA (North American Land Mammal Age).

	Hemphillian		Blancan		Irvingtonian		Rancholabrean	
	<i>Mylohyus</i>	<i>Protherohyus</i>	<i>Mylohyus</i>	<i>Platygonus</i>	<i>Mylohyus</i>	<i>Platygonus</i>	<i>Mylohyus</i>	<i>Platygonus</i>
n	7	8	3	8	10	33	29	17
Mean	−13.5	−10.6	−13.9	−12.8	−10.6	−10.0	−11.0	−13.0
Median	−13.8	−11.1	−14.0	−12.9	−11.6	−10.1	−11.5	−13.1
SD	2.4	2.5	1.0	0.9	2.4	2.8	2.2	1.7
Maximum	−8.6	−7.3	−12.9	−11.5	−6.4	−4.8	−3.8	−9.4
Minimum	−15.8	−13.6	−14.9	−14.6	−13.7	−14.2	−13.6	−15.4
Range	7.2	6.3	2.0	3.1	7.3	9.4	9.8	6.0

n is sample size; SD, standard deviation (n − 1); Range, total range of all samples examined. Values have been corrected for the Suess effect (−1.5 ‰ in extinct taxa as compared to modern taxa).

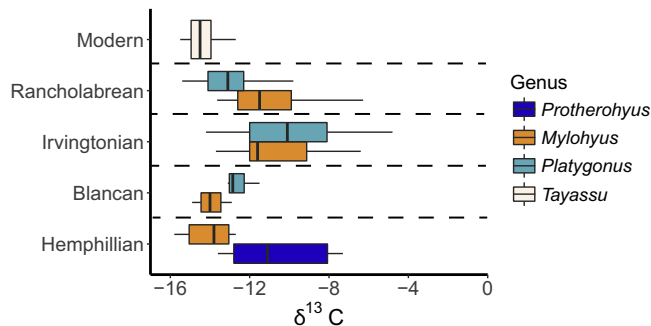


Fig. 2. Boxplot of stable carbon isotope values separated by NALMA for co-occurring Tayassuidae genera. All stable carbon values for extinct genera have been adjusted by −1.5‰ to account for increased emissions since the industrial revolution (Cerling et al., 1997; Cerling and Harris, 1999; Passey et al., 2005). The single line within each box represents the median value, while the left and right boundaries of the box represent the first and third quartiles, respectively. Lines extending perpendicularly from the outer boundaries of the box encompass data falling outside of the first and third quartiles, with the end points of these lines not exceeding 1.5 × inner quartile range (distance between lower and upper quartile). Isolated black dots are outliers.

has more bunodont teeth, which are well suited for crushing and grinding, while *Platygonus* has sheering crests on their teeth, which suggest a more folivorous or tough-food diet (Webb, 1974). Overall, isotopic ranges for both genera suggest *Platygonus* and *Mylohyus* consumed C₃ and C₄ plant material in Florida (Table 4; Cerling et al., 1997; Cerling and Harris, 1999).

Stable carbon isotope values from both genera become significantly higher and indistinguishable from one another during the Irvingtonian (Table S8), suggesting *Platygonus* and *Mylohyus* shifted their diet from primarily C₃ browse towards more of a mixed diet. Further, isotope values for the two genera were indistinguishable from one another, indicating both genera potentially foraged in similar habitats. During the Rancholabrean, *Mylohyus* continued to consume harder food items in more open environments than *Platygonus*, as evidenced by higher *Asfc* values and greater stable carbon isotope values for *Mylohyus* (Fig. 2).

Throughout the Pleistocene, *Platygonus* does not alter the textural properties of food items consumed and during all times is consuming tough foods (e.g., tough leaves and/or grass). However, *Platygonus* is interpreted as a C₃ browser in the early and late Pleistocene but a mixed C₃/C₄ feeder in the mid Pleistocene (Irvingtonian), demonstrating variability in dietary behavior including potential food or habitat preferences. The environment during the Irvingtonian may have been more open than the earlier or later Pleistocene as indicated by higher δ¹³C values from both *Platygonus* and *Mylohyus* during this time period, and previous studies (DeSantis et al., 2009). This may suggest that *Platygonus* was primarily a C₃ browser, but was able to fluctuate diet during times of increased aridity.

All tayassuid mean isotope values are below −9‰ suggesting that none of the peccaries in this study had a primarily C₄ grazing diet; however, higher isotopic values indicate at least some C₄ resources were consumed by *Platygonus* and *Mylohyus*. Further, *Mylohyus* was not restricted to the forest in terms of food consumption during the Irvingtonian and Rancholabrean NALMAs, as δ¹³C values are representative of a broader diet including both C₃ and C₄ resources during these time periods. With the exception of the Irvingtonian, when *Platygonus* and *Mylohyus* are eating both C₃ and C₄ food sources, δ¹³C values for *Platygonus* are consistent with those of a predominantly C₃ browser. Over the past 2.5 million years, the paleoclimate of Florida has been consistently somewhat warm and humid, as evidenced by the consistent presence of alligators and land tortoises (Hulbert, 2001), though some periods reflect glacial times when climates were dryer and/or cooler with associated sea-level fluctuations (DeSantis et al., 2009; Hulbert, 2001; Yann and DeSantis, 2014). The transition from lower δ¹³C values in the Hemphillian and Blancan to higher values in the Irvingtonian is consistent with prior studies documenting that some Irvingtonian sites occurred during interglacial periods and were subjected to increased evapotranspiration (DeSantis et al., 2009; Yann et al., 2013). Lower δ¹³C values in the Rancholabrean suggest a return to consuming vegetation in more closed environments, despite some sites occurring during times with increased evapotranspiration (Yann and DeSantis, 2014).

Previous studies have hypothesized that more generalized dietary behavior may have been key to surviving the end Pleistocene extinction (e.g. DeSantis and Haupt, 2014). Therefore, it is also interesting to note that both *Mylohyus* and *Platygonus*, taxa that have demonstrated the ability to alter diet in response to changing climate, become extinct at the end Pleistocene. Thus, perhaps the ability to alter diet was not a sufficient survival mechanism for tayassuids and additional selective pressures, such as increased predation (e.g. Surovell and Waguespack, 2009), were driving factors in their extinction.

5.2. Modern peccaries

All three genera of extinct peccaries exhibit higher mean isotopic values as compared to modern *Tayassu* (Tables 4–5). This may be due either to the extinct peccaries having more generalized diets or an impact of canopy-cover, which can be greater in tropical as compared to temperate latitudes (Canham et al., 1990). Further, there are no differences in the textural properties of food items consumed between *Tayassu* and any of their extinct relatives (Table 2, Fig. 1), suggesting that *Tayassu* consume similar food items in terms of texture (i.e. abrasiveness and hardness). Low mean carbon isotope values and relatively high complexity values similar to those of the extinct peccaries, indicate modern *Tayassu* exhibit similar diets to their extinct counterparts and are primarily C₃ frugivores/folivores/browsers, consistent with modern ecological studies evaluating diet (e.g. Altrichter et al., 2001; Beck, 2005; Keuroghlian and Eaton, 2008). A narrow range of *Tayassu* carbon

isotope values (Table 4) may insinuate that modern tayassuids have a more restrictive diet, isotopically, or potentially have a large range of food items available within a narrow range of isotopic values. As modern ecological studies note, *Tayassu* consume a wide variety of food items based on seasonal availability (Keuroghlian et al., 2009). Based on isotopic data here discussed, variations in diet during times of food scarcity likely do not include C₄ plant material as a food source, thus limiting total isotopic variability.

It is important to note that our results may be a conservative estimate of stable carbon isotope values for *Tayassu*. All specimens analyzed here were recovered from central Brazil, and all but five occurred in the Cerrado and Pantanal biomes, an interior tropical forest and seasonally inundated wetland, respectively (Olson et al., 2001). We anticipate, however, that stable carbon values from the enamel of peccaries in a denser tropical rainforest, such as the Atlantic Forest or the Amazon (Olson et al., 2001), would result in more negative values than are indicated here. Therefore, the carbon values from modern *Tayassu* enamel as noted in this study may be interpreted as a minimum estimate of differences between extant and extinct peccaries. In addition, comparisons between extinct and extant peccaries may also be somewhat reflective of the time averaging, as extant samples are from a more temporally narrow time frame. Future work that assesses how extinct peccaries compare to the extant collared peccary (*Pecari tajacu*) and the chacoan peccary (*Catagonus wagneri*) can help clarify if and how dietary variability as inferred from stable isotopes and dental microwear has changed for the Tayassuidae as a whole, as opposed to one specific genus.

6. Conclusions

Here, we assessed the degree of dietary variability among extinct peccaries in Florida to understand whether extinct peccaries were able to fluctuate diet in times of changing climate and to use this information as a proxy for understanding how modern taxa may respond to climate changes. In Florida, both *Mylohyus* and *Platygonus* shift from consuming predominantly C₃ vegetation to a mixed diet of C₃ and C₄ vegetation over time, while *Protherohyus* consumed vegetation in more open areas during the Hemphillian when C₄ grasses were beginning to expand globally (Cerling et al., 1997). In contrast, modern *Tayassu* show no indication of mixed-feeding and instead consume primarily C₃ resources in more closed environments, even in more open biomes such as the Cerrado and the Pantanal. The diet of *Tayassu* may be a function of a shift in dietary preferences in the present day, as compared to their extinct counterparts. While it is unclear if and how *Tayassu* will alter diets with changing climates, like their extinct predecessors, tayassuids did fluctuate their diet over time and may be more adaptable than other co-occurring taxa.

Acknowledgments

We would like to thank Greg Smith, Brent Jones, and Jonathan Crites for input and assistance with scanning peccary teeth. This project would not be possible without the MZUSP and FLMNH for graciously allowing access to their specimens and to Richard Hulbert for sharing his detailed and extensive knowledge of the Tayassuidae in Florida. We are grateful to Sean Keuroghlian-Eaton for help in the field as well as assistance preparing modern *Tayassu* teeth for DMTA and isotopic analysis. We also thank four anonymous reviewers for their detailed feedback and comments that greatly improved this manuscript. This work was supported by a GSA student grant (No. 15041433 to Bradham), Vanderbilt University, and NSF (EAR 1053839 to DeSantis).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2018.03.020>.

References

- Altrichter, M., Boaglio, G.I., 2004. Distribution and relative abundance of peccaries in the Argentine Chaco: associations with human factors. *Biol. Conserv.* 116, 217–225. [http://dx.doi.org/10.1016/S0006-3207\(03\)00192-7](http://dx.doi.org/10.1016/S0006-3207(03)00192-7).
- Altrichter, M., Carrillo, E., Sáenz, J., Fuller, T.K., 2001. White-lipped peccary (*Tayassu pecari*, Artiodactyla: Tayassuidae) diet and fruit availability in a Costa Rican rain forest. *Rev. Biol. Trop.* 49, 1183–1192.
- Barreto, G., Hernandez, O., Ojasti, J., 1996. Diet of peccaries (*Tayassu tajacu* and *T. pecari*) in a dry forest of Venezuela. *J. Zool. Soc. London* 241, 279–284.
- Beck, H., 2005. Seed predation and dispersal by peccaries throughout the Neotropics and its consequences: a review and synthesis. In: *Seed Fate: Predation, Dispersal and Seedling Establishment*. CABI Publishing, Wallingford, UK, pp. 77–115.
- Beck, H., 2006. A review of peccary–palm interactions and their ecological ramifications across the Neotropics. *J. Mammal.* 87, 519–530. <http://dx.doi.org/10.1644/05-MAMM-A-174R1.1>.
- Bodmer, R.E., 1990. Ungulate frugivores and the browser-grazer continuum. *Oikos* 57, 319–325.
- Calandra, I., Merceron, G., 2016. Dental microwear texture analysis in mammalian ecology. *Mamm. Rev.* 46, 215–228. <http://dx.doi.org/10.1111/mam.12063>.
- Campbell, K., Prothero, D., Romero-Pittman, L., Hertel, F., Rivera, N., 2010. Amazonian magnetostratigraphy: dating the first pulse of the Great American Faunal Interchange. *J. S. Am. Earth Sci.* 29, 619–626.
- Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. For. Res.* 20, 620–631. <http://dx.doi.org/10.1139/x90-084>.
- Cerling, T.E., Harris, J.M., 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120, 347–363. <http://dx.doi.org/10.1007/s004420050868>.
- Cerling, T.E., Harris, J.M., Macfadden, B.J., Leakey, M.G., Quadek, J., Eisenmann, V., Ehleringer, J.R., 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389, 153–158. <http://dx.doi.org/10.1038/38229>.
- Cerling, T.E., Hart, J.A., Hart, T.B., 2004. Stable isotope ecology in the Ituri Forest. *Oecologia* 138, 5–12. <http://dx.doi.org/10.1007/s00442-003-1375-4>.
- Cione, A.L., Gasparini, G.M., Soibelzon, E., Soibelzon, L.H., Tonni, E.P., 2015. The Great American Biotic Interchange: A South American Perspective. Springer, Dordrecht. <http://dx.doi.org/10.1007/978-94-017-9792-4>.
- Coplen, T.B., 1994. Reporting of stable hydrogen, carbon, and oxygen isotopic abundances. *Pure Appl. Chem.* 66, 273–276.
- D'Amo, P., 2001. Paleofaunal, Paleodietary and Paleoenvironmental Study of Cutler Hammock: A Cave Deposit from the Late Pleistocene of Florida. University of Florida.
- DeSantis, L.R.G., 2016. Dental microwear textures: reconstructing diets of fossil mammals. *Surf. Topogr. Metrol. Prop.* 4, 023002. <http://dx.doi.org/10.1088/2051-672X/4/2/023002>.
- DeSantis, L.R.G., Haupt, R.J., 2014. Cougars' key to survival through the Late Pleistocene extinction: insights from dental microwear texture analysis. *Biol. Lett.* 10.
- DeSantis, L.R.G., Wallace, S.C., 2008. Neogene forests from the Appalachians of Tennessee, USA: geochemical evidence from fossil mammal teeth. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 266, 59–68. <http://dx.doi.org/10.1016/j.palaeo.2008.03.032>.
- DeSantis, L.R.G., Feranec, R.S., MacFadden, B.J., 2009. Effects of global warming on ancient mammalian communities and their environments. *PLoS One* 4, 2–8. <http://dx.doi.org/10.1371/journal.pone.0005750>.
- DeSantis, L.R.G., Scott, J.R., Schubert, B.W., Donohue, S.L., McCray, B., Van Stolk, C., Winburn, A., Greschko, M., O'Hara, M., 2013. Direct comparisons of 2D and 3D dental microwear proxies in extant herbivores and carnivorous mammals. *PLoS One* 8, e71428.
- DeSantis, L.R.G., Field, J., Wroe, S., Dodson, J., 2017. Dietary response of Sahul (Pleistocene Australia-New Guinea) megafauna to climate and environmental change. *Paleobiology* 43, 181–195.
- Desbiez, A.L.J., Santos, S.A., Keuroghlian, A., Bodmer, R.E., 2009. Niche partitioning among white-lipped peccaries (*Tayassu pecari*), collared peccaries (*Pecari tajacu*), and feral pigs (*Sus Scrofa*). *J. Mammal.* 90, 119–128. <http://dx.doi.org/10.1644/08-MAMM-A-038.1>.
- Dunn, O., 1964. Multiple comparisons using rank sums. *Technometrics* 6, 241–252.
- Feranec, R.S., 2005. Growth rate and duration of growth in the adult canine of *Smilodon gracilis*, and inferences on diet through stable isotope analysis. *Bull. Florida Museum Nat. Hist.* 45, 369–377.
- Feranec, R.S., DeSantis, L.R.G., 2014. Understanding specifics in generalist diets of carnivores by analyzing stable carbon isotope values in Pleistocene mammals of Florida. *Paleobiology* 40, 477–493. <http://dx.doi.org/10.1666/13055>.
- Feranec, R.S., MacFadden, B.J., 2000. Evolution of the grazing niche in Pleistocene mammals from Florida: evidence from stable isotopes. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 162, 155–169. [http://dx.doi.org/10.1016/S0031-0182\(00\)00110-3](http://dx.doi.org/10.1016/S0031-0182(00)00110-3).
- Fragoso, M., 1994. Large Mammals and the Community Dynamics of an Amazonian Rain Forest. University of Florida, Gainesville.
- Fragoso, J.M., 1998. Home range and movement patterns of white-lipped peccary (*Tayassu pecari*) herds in the northern Brazilian Amazon. *Biotropica* 30, 458–469. <http://dx.doi.org/10.1111/j.1744-7429.1998.tb00080.x>.
- Gasparini, G.M., 2013. Records and stratigraphical ranges of South American Tayassuidae (Mammalia Artiodactyla). *J. Mamm. Evol.* 20, 57–68. <http://dx.doi.org/10.1007/s10914-011-9172-z>.
- Gongora, J., Moran, C., 2005. Nuclear and mitochondrial evolutionary analyses of collard, white-lipped, and Chacoan peccaries (Tayassuidae). *Mol. Phylogenet. Evol.* 34, 181–189.

- Grine, F.E., 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. *J. Hum. Evol.* 15, 783–822. [http://dx.doi.org/10.1016/S0047-2484\(86\)80010-0](http://dx.doi.org/10.1016/S0047-2484(86)80010-0).
- Grine, F., Ungar, P., Teaford, M., 2002. Error rates in dental microwear quantification using scanning electron microscopy. *Scanning* 24, 144–153.
- Hedberg, C., DeSantis, L., 2017. Dental microwear texture analysis of extant koalas: clarifying causal agents of microwear. *J. Zool.* 301, 206–214. <http://dx.doi.org/10.1111/jzo.12413>.
- Hoppe, K.A., Stover, S.M., Pascoe, J.R., Amundson, R., 2004. Tooth enamel biomineralization in extant horses: implications for isotopic microsampling. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 206, 355–365. <http://dx.doi.org/10.1016/j.palaeo.2004.01.012>.
- Hulbert, R., 2001. *The Fossil Vertebrates of Florida*. University Press of Florida (384 pp).
- Hulbert, R.C., Morgan, G.S., Kerner, A., 2009. Collared peccary (Mammalia, Artiodactyla, Tayassuidae, *Pecari*) from the Late Pleistocene of Florida. *Pap. Geol. Vertebr. Paleontol. Biostatigraphy Honor Michael O. Woodburne. Museum North. Arizona Bull.* 65, Flagstaff, Arizona. pp. 543–556.
- IUCN, 2017. The IUCN Red List of Threatened Species. www.IUCNredlist.org.
- Janis, C.M., Damuth, J., Theodor, J.M., 2002. The origins and evolution of the North American grassland biome: the story from the hoofed mammals. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 177, 183–198. [http://dx.doi.org/10.1016/S0031-0182\(01\)00359-5](http://dx.doi.org/10.1016/S0031-0182(01)00359-5).
- Jansen, P., 2003. *Scatterhoarding and Tree Regeneration: Ecology of Nut Dispersal in a Neotropical Rainforest*. Wageningen University, Wageningen, The Netherlands.
- Jones, D.B., DeSantis, L., 2017. Dietary ecology of ungulates from the La Brea tar pits in southern California: a multi-proxy approach. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 466, 110–127. <http://dx.doi.org/10.1016/j.palaeo.2016.11.019>.
- Kaiser, T.M., Schulz, E., 2006. Tooth wear gradients in zebras as an environmental proxy - a pilot study. *Mitt. hamb. zool. Mus. Inst.* 103, 187–211.
- Keuroghlian, A., Eaton, D.P., 2008. Fruit availability and peccary frugivory in an isolated Atlantic forest fragment: effects on peccary ranging behavior and habitat use. *Biotropica* 40, 62–70. <http://dx.doi.org/10.1111/j.1744-7429.2007.00351.x>.
- Keuroghlian, A., Eaton, D.P., Desbiez, A., 2009. The response of a landscape species, white-lipped peccaries, to seasonal resource fluctuations in a tropical wetland, the Brazilian Pantanal. *Int. J. Biodivers. Conserv.* 1, 87–97.
- Kiltie, R., 1981a. Distribution of palm fruits on a rain forest floor: why white-lipped peccaries forage near objects. *Biotropica* 141–145.
- Kiltie, R., 1981b. Stomach contents of rain forest peccaries (*Tayassu tajacu* and *T. pecari*). *Biotropica* 13, 234–236.
- Koch, P.L., Hoppe, K.A., Webb, S.D., 1998. The isotopic ecology of late Pleistocene mammals in North America Part 1. *Florida. Chem. Geol.* 152, 119–138. [http://dx.doi.org/10.1016/S0009-2541\(98\)00101-6](http://dx.doi.org/10.1016/S0009-2541(98)00101-6).
- Kohn, M., 2010. Carbon isotope compositions of terrestrial C3 plants as indicators of (paleo) ecology and (paleo) climate. *Proc. Natl. Acad. Sci.* 107, 19691–19695.
- MacFadden, B.J., Cerling, T.E., 1996. Mammalian herbivore communities, ancient feeding ecology, and carbon isotopes: a 10-million-year sequence from the Neogene of Florida. *J. Vertebr. Paleontol.* 16, 103–115.
- Merceron, G., Ramdarshan, A., Francisco, A., Gautier, D., Boissier, J., Milhet, X., Novello, A., Pret, D., 2016. Untangling the environmental from the dietary: dust does not matter. *Proc. R. Soc. B Biol. Sci.* 283, 20161032. <http://dx.doi.org/10.6084/m9.figshare.c.3461769>.
- van der Merwe, N.J., Medina, E., 1989. Photosynthesis and ratios in Amazonian rain forests. *Geochim. Cosmochim. Acta* 53, 1091–1094. [http://dx.doi.org/10.1016/0016-7037\(89\)90213-5](http://dx.doi.org/10.1016/0016-7037(89)90213-5).
- van der Merwe, N.J., Medina, E., 1991. The canopy effect, carbon isotope ratios and foodwebs in Amazonia. *J. Archaeol. Sci.* 18, 249–259.
- Mihlbachler, M.C., Beatty, B.L., 2012. Magnification and resolution in dental microwear analysis using light microscopy. *Palaeontol. Electron.* 15, 1–15.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R., 2001. Terrestrial ecoregions of the world: a new map of life on earth. *Bioscience* 51, 933. [http://dx.doi.org/10.1641/0006-3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](http://dx.doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2).
- Parisi Dutra, R., de Melo Casali, D., Velloso Missaglia, R., Gasparini, G., Perini, F., Cozzuol, M., 2017. Phylogenetic systematics of peccaries (Tayassuidae: Artiodactyla) and a classification of South American Tayassuids. *J. Mamm. Evol.* 24, 345–358.
- Passey, B.H., Robinson, T.F., Ayliffe, L.K., Cerling, T.E., Sponheimer, M., Dearing, M.D., Roeder, B.L., Ehleringer, J.R., 2005. Carbon isotope fractionation between diet, breath CO₂, and bioapatite in different mammals. *J. Archaeol. Sci.* 32, 1459–1470. <http://dx.doi.org/10.1016/j.jas.2005.03.015>.
- Prideaux, G.J., Ayliffe, L.K., DeSantis, L.R.G., Schubert, B.W., Murray, P.F., Gagan, M.K., Cerling, T.E., 2009. Extinction implications of a chenopod browse diet for a giant Pleistocene kangaroo. *Proc. Natl. Acad. Sci. U. S. A.* 106, 11646–11650. <http://dx.doi.org/10.1073/pnas.0900956106>.
- Prothero, D., 2015. *Evolution of the early Miocene Hesperhine peccaries*. *New Mexico Mus. Nat. Hist. Sci. Bull.* 67, 235–256.
- R Core Team, 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria URL. <http://www.R-project.org/>.
- Reyna-Hurtado, R., Beck, H., Altrichter, M., Chapman, C.A., Bonnell, T.R., Keuroghlian, A., 2015. What Ecological and Anthropogenic Factors Affect Group Size in White-lipped Peccaries (*Tayassu pecari*)? 0. pp. 1–9. <http://dx.doi.org/10.1111/btp.12269>.
- Schmidt, C.W., 2008. Dental microwear analysis of extinct flat-headed peccary (*Platygonus compressus*) from southern Indiana. *Proc. Indiana Acad. Sci.* 117, 95–106.
- Scott, J., 2012. Dental microwear texture analysis of extant African Bovidae. *Mammalia* 76, 157–174.
- Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Grine, F.E., Teaford, M.F., Walker, A., 2005. Dental microwear texture analysis shows within-species diet variability in fossil hominins. *Nature* 436, 693–695. <http://dx.doi.org/10.1038/nature03822>.
- Scott, R.S., Ungar, P.S., Bergstrom, T.S., Brown, C.A., Childs, B.E., Teaford, M.F., Walker, A., 2006. Dental microwear texture analysis: technical considerations. *J. Hum. Evol.* 51, 339–349. <http://dx.doi.org/10.1016/j.jhevol.2006.04.006>.
- Semprebon, G.M., Godfrey, L.R., Solounias, N., Sutherland, M.R., Jungers, W.L., 2004. Can low-magnification stereomicroscopy reveal diet? *J. Hum. Evol.* 47, 115–144. <http://dx.doi.org/10.1016/j.jhevol.2004.06.004>.
- Silvius, K.M., 2002. Spatio-temporal patterns of palm endocarp use by three Amazonian forest mammals: granivory or “grubivory”? *J. Trop. Ecol.* 18, 707–723. <http://dx.doi.org/10.1017/S0266467402002468>.
- Solounias, N., Semprebon, G., 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. *Am. Museum Novit.* 3366, 1–49. [http://dx.doi.org/10.1206/0003-0082\(2002\)366<0001:AITROU>2.0.CO;2](http://dx.doi.org/10.1206/0003-0082(2002)366<0001:AITROU>2.0.CO;2).
- Sowls, L., 1984. *The Peccaries*. University of Arizona Press, Tucson.
- Stowe, T., Teeri, J., 1978. Geographic distribution of C4 species of the Dicotyledonae in relation to climate. *Am. Nat.* 112, 609–623.
- Strait, S.G.S., 1997. Tooth use and the physical properties of food. *Evol. Anthropol. Issues. News. Rev.* 5, 199–211. [http://dx.doi.org/10.1002/\(sici\)1520-6505\(1997\)5:6<199::aid-evan2>3.0.co;2-8](http://dx.doi.org/10.1002/(sici)1520-6505(1997)5:6<199::aid-evan2>3.0.co;2-8).
- Surovell, T., Waguespack, N.M., 2009. Human prey choice in the late Pleistocene and its relation to megafaunal extinctions. *Am. Megafaunal Extinctions End Pleistocene* 77–105.
- Teeri, J., Stowe, L., 1976. Climatic patterns and the distribution of C4 grasses in North America. *Oecologia* 23.
- Torres, R., Tamburini, D., Lescano, J., Rossi, E., 2016. New records of the endangered Chacoan peccary *Catagonus wagneri* suggest a broader distribution than formerly known. *Oryx* 51, 1–4. <http://dx.doi.org/10.1017/S0030605315001404>.
- Traylor, R.B., Dundas, R.G., Fox-Dobbs, K., Van De Water, P.K., 2015. Inland California during the Pleistocene-Megafaunal stable isotope records reveal new paleoecological and paleoenvironmental insights. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 437, 132–140. <http://dx.doi.org/10.1016/j.palaeo.2015.07.034>.
- Ungar, P.S., Brown, C.A., Bergstrom, T.S., Walker, S.A., 2003. Quantification of dental microwear by tandem scanning confocal microscopy and scale-sensitive fractal analyses. *Scanning* 25, 185–193.
- Walker, A., Hoeck, H., Perez, L., 1978. Microwear of mammalian teeth as an indicator of diet. *Science* 201, 908–910.
- Webb, D., 1974. *Pleistocene Mammals of Florida*. University Press of Florida.
- Webb, S., Hulbert, R., Morgan, G., Evans, H., 2008. Terrestrial mammals of the Palmetto Fauna (early Pliocene, latest Hemphillian) from the central Florida phosphate district. *Nat. Hist. Mus. LA. County. Sci. Series* 41, 293–312.
- Wetzel, R.M., Dubos, R.E., Martin, R.L., Myers, P., Ward, W.R., 1975. *Catagonus*, an “extinct” peccary, alive in Paraguay. *Science* 189, 379–381.
- Wright, D., 1989. Phylogenetic relationships of *Catagonus wagneri*: sister taxa from the tertiary of North America. In: Redford, K. (Ed.), *Advances in Neotropical Mammalogy*. Sandhill Crane Press, Gainesville, pp. 281–308.
- Wright, D., 1998. Tayassuidae. In: Janis, C.M., Scott, K., Jacobs, L. (Eds.), *Evolution of Tertiary Mammals of North America. Terrestrial Carnivores, Ungulates, and Ungulate-like Mammals Vol. 1*. Cambridge University Press, Cambridge, pp. 389–401.
- Yann, L.T., DeSantis, L.R.G., 2014. Effects of Pleistocene climates on local environments and dietary behavior of mammals in Florida. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 414, 370–381. <http://dx.doi.org/10.1016/j.palaeo.2014.09.020>.
- Yann, L.T., DeSantis, L.R.G., Haupt, R.J., Romer, J.L., Corapi, S.E., Ettenson, D.J., 2013. The application of an oxygen isotope aridity index to terrestrial paleoenvironmental reconstructions in Pleistocene North America. *Paleobiology* 39, 576–590. <http://dx.doi.org/10.1666/12059>.
- Yann, L., DeSantis, L., Koch, P.L., Lundelius, E., 2016. Dietary ecology of Pleistocene camelids: influences of climate, environment, and sympatric taxa. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 461, 389–400.